NEW TRIBAL PLACEMENT OF THE GENUS COSCINOCEPHALUS PRELL, 1936, WITH DESCRIPTION OF THE LARVA, PUPA AND ADULT OF A NEW SPECIES FROM MEXICO (COLEOPTERA: SCARABAEOIDEA; DYNASTINAE)

MIGUEL A. MORÓN AND BRETT C. RATCLIFFE

¹Departamento de Biosistemática de Insectos, Instituto de Ecología, A.C. A.P. 63 Xalapa, Veracruz 91000 México

²Systematics Research Collections, W436 Nebraska Hall University of Nebraska, Lincoln, NE 68588-0514, U.S.A.

Abstract.—A discussion is presented suggesting the transfer of Coscinocephalus from the Cyclocephalini to the Pentodontini. Coscinocephalus tepehuanus is described as new, based on immature and adult forms, from Durango state, Mexico. A key to the third-stage larvae of nine genera of American Pentodontini is presented. Finally, a brief commentary is given about life history information.

Resúmen.—Se presenta una discusión para justificar la transferencia del género Coscinocephalus de la tribu Cyclocephalini a la tribu Pentodontini. Se describe Coscinocephalus tepehuanus n. sp. con base en 6 adultos, así como su larva de tercer estadio y la pupa, recolectados
en un bosque de pinos y encinos del estado de Durango, México. Se incluyen: una clave para
separar las dos especies conocidas del género, una clave para las larvas de tercer estadio de 9
géneros de Pentodontini americanos y un comentario breve sobre los hábitos de estas especies.

Some genera of American Dynastinae have restricted geographical ranges and/or ecological tolerances, such as *Aphonides* Rivers, *Pentodina* Endrödi, *Coscinoce-phalus* Prell, *Barutus* Ratcliffe, *Tehuacania* Endrödi, *Gillaspytes* Howden, *Hiekei-anus* Endrödi, *Neoryctes* Arrow, *Surutoides* Endrödi, *Indieraligus* Dechambre, and *Endroedianibe* Chalumeau. Some of these genera are also monotypic, with insular habitats or extreme vicariant relatives and are usually very rare in collections. It is possible that most of these genera represent relictual elements that may provide useful data for phyletic studies of the subfamily.

Recent collecting trips (both in the field and in collections) have given us new information on the controversial genus *Coscinocephalus*. Thus, the purposes of this paper are: (1) to justify the tribal transfer of *Coscinocephalus* from Cyclocephalini to Pentodontini; (2) to describe a new species from Mexico; (3) to describe the third-stage larva and pupa of the new species; (4) to update the known distribution of the genus; (5) to discuss the habits of the species; and (6) to provide a key to the known third-stage larvae of American Pentodontini. Technical terms used are those of Ritcher (1966), Morón (1987) and Costa *et al.* (1988).

Anoplocephalus cribrifrons was described by Schaeffer (1906) but the genus was preoccupied by Anoplocephalus Henrick 1895 (Platyhelminthes: Cestoda). Prell (1936) provided the replacement name Coscinocephalus. Schaeffer indicated the difficulty of placing the genus in a tribe using the then present classification. He stated

that "this genus is intermediate between Lacordaire's 'Cyclocephalides' and 'Oryctides'."

"Pentodontidae" was originally proposed by Burmeister (1847), but it was seemingly not widely used in classifications even though Bates (1888) adhered to it in the Biologia. It is easy to understand Schaeffer's indecision (especially if he was unfamiliar with Burmeister's work) when he had only the old *descriptions* of the "Cyclocephalides" or "Oryctides" by which to place the new genus, and neither one seemed to properly accommodate *Anoplocephalus*.

It was not until Casey (1915), nine years after the description of *Anoplocephalus*, that Pentodontini made its way into the primary North American literature. The tribe again fell into obscurity when it was not used in Leng's (1920) catalog of North American Coleoptera, Arrow's (1937) Coleopterorum Catalogus, Blackwelder's (1944) checklist of the Coleoptera of Latin America, or Arnett's (1968) beetles of the United States. Endrödi (1969, 1985) reinstated the use of Pentodontini and provided the first modern definition of it. The definition, however, leaves a lot to be desired because monophyly was not addressed; some concerns remain that the Pentodontini (as currently comprised) may be paraphyletic.

Adult pentodontines are distinguished by the presence of tubercles, carinae, or a fovea on the head and/or pronotum; mandibles on the lateral margin with or without teeth; propygidium with or without a stridulatory structure; protibiae usually tridentate, and apex of the metatibiae usually truncate and margined with short, spine-like setae. Dimorphism between the males and females is slight.

The larvae are characterized by 1–3 dorsal sensory spots on the last antennal segment; the molar area of the left mandible is dentate or, if lacking teeth, then the stridulatory teeth of the maxilla have acute projections directed distally; and the raster has one or more rows of palidia or, if lacking the palidia, then the chaetoparia of the epipharynx has few setae.

Some adults in the Pentodontini are similar to others in the Oryctini. The two tribes (as currently structured) may generally be separated by the presence of a truncate or nearly smooth apical rim on the apex of the posterior tibia in the pentodontines and by a toothed (including apical tooth) or strongly crenulate rim in the oryctines. As opposed to the Cyclocephalini, all pentodontines have at least some head or pronotal armature in the form of carinae, tubercles, or even horns.

It appears that Casey (1915) was the first to definitively place the then Anoplocephalus in the Cyclocephalini. Endrödi (1969, 1985) maintained its position in the Cyclocephalini based on the absence of head and pronotal armature and the presence of slender legs. In this regard, however, it should be noted that both species of Coscinocephalus possess as much of a developed boss, or tubercle, on the frons as in species of Orizabus, Pentodina, or Euetheola in the Pentodontini. The slender, long legs seem to be a variable character within tribes. In this case, we believe it is correlated with the arboreal habits of Coscinocephalus species. By contrast, most members of the Pentodontini have soil burrowing habits and have stouter (though not truly fossorial) legs.

We believe that *Coscinocephalus* is more appropriately placed in the Pentodontini for the following reasons: (1) the head is "armed"; (2) the mandibles, labrum, and maxilla are all relatively simple or small, and the labium is strongly constricted apically as in *Orizabus* (but unlike the general state found in the Cyclocephalini).

See Table 1 for further comparisons; (3) the clypeus is strongly bilobed and reflexed as in *Orizabus* but unlike any other Cyclocephalini; (4) the form of the parameres is more elongated, slender, and setose as in other Pentodontini but especially as in *Orizabus*; (5) the characters of the mouthparts in the larvae of *Coscinocephalus*, while showing no clear affinity (Table 2), are not like those of Cyclocephalini.

Our study of both adult and larval features leads us to conclude that *Coscinoce-phalus* is not a cyclocephaline. In most respects the adults seem to be more closely related to *Orizabus* in the Pentodontini while the larvae share some affinities with larvae of *Xyloryctes* in the Oryctini. Even though we have some reservations about the monophyly of each of these tribes, we here place *Coscinocephalus* in the tribe Pentodontini.

We have thus come full circle to Schaeffer's (1906) original feeling that "this genus is intermediate between Lacordaire's 'Cyclocephalides' and 'Oryctides'." The Pentodontini, a concept unknown or unrecognized by Schaeffer, is the intermediate between the Cyclocephalini and the Oryctini, and it is here that we place *Coscinocephalus*.

Coscinocephalus tepehuanus Morón and Ratcliffe, new species (Figs. 1–8)

Type series: Holotype labeled "México: Durango, Res. Biosfera 'La Michilía,' alt. 2,400 m, R. Terrón col., pino-encino, ex larva, 24-X-87, adulto 10-IV-88, suelo cerca raíces *Quercus durifolia*." Allotype labeled "México: Durango, Súchil, Piedra Herrada. Res. Biosfero 'La Michilía,' alt. 2,400 m, 16-VIII-79, bosque *Quercus-Pinus*, sobre suelo, M.A. Morón col." Four paratypes with the following data: as holotype except without date of adult eclosion (1 male), as allotype except 10-VII-86 and "caminando en suelo, después de lluvia, 17 hrs. R.A. Terrón Sierra col." (2 females); "Mexico: Durango, Súchil, Res. Biosfera 'La Michilía,' Rcho. de la Peña, 26-VII-78, R. Halffter col., luz, bosque *Pinus-Quercus*, alt. 2,400 m" (1 male).

The pupal and third instar exuviae are also present for the holotype and one male paratype.

Holotype and allotype deposited in the Miguel A. Morón collection (at the Instituto de Ecología, Xalapa); two paratypes (male and female) deposited at the Instituto de Biología, UNAM collection (Mexico City); remaining male and female paratypes in the B.C. Ratcliffe collection (Lincoln).

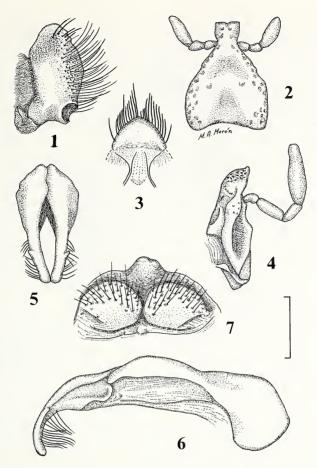
Holotype: Male. Length 21.5 mm from apex of clypeus to apex of elytra; width across humeri 11.2 mm. Color uniformly light reddish brown, moderately shining. *Head:* Clypeus with sides sinuate, converging to broad, bilobed apex; sides and apex strongly reflexed; surface densely rugopunctate. Vertex with large, oblong to transverse punctures. Low, rounded boss on frons between eyes. Interocular width equals 3.8 transverse eye diameters. Eye canthus with ventrolateral row of long, stout setae projecting laterally. Antenna with 10 segments, club subequal in length to segments 2–7. Mandibles (Fig. 1) small, not visible from above, lacking teeth, lateral edge with row of large setae, molar area small. Labium (Fig. 2) strongly contracted to small, narrow, feebly emarginate apex; lateral edges with stout setae (as long or longer than palps); ventral surface in basal half strongly and broadly depressed. Labrum (Fig. 3) small, subtriangular. Maxilla (Fig. 4) with small, subtriangular, se-

Table 1. General structure of adult mouthparts in 7 species of Dynastinae.

SPECIES	Labrum	Mandible	Maxilla	Labium
Cyclocephala maffafa	Wide; with condyla	Apex elbowed, without teeth; molar area wide	With 5 acute teeth	Anterior border wide, curved
Ancognatha manca	Wide; with condyla	Apex curved, without teeth; molar area wide	With 1 acute tooth	Anterior border wide, sinuated
Paraspidolea fuliginea	Wide; with condyla	Apex curved, without teeth; molar area wide	With 2 short teeth; long brush of setae	Anterior border wide, sinuated
Coscinocephalus tepe- huanus	Narrow; without condyla	Apex rounded, without teeth; molar area small	Without teeth or brush of setae	Anterior border narrow, truncated
Orizabus brevicollis	Narrow; without condyla	Apex rounded, without teeth; molar area small	With 5 acute teeth	Anterior border narrow, truncated
Ligyrus bituberculatus	Wide; with condyla	Apex with 2 acute teeth; molar area wide	With 6 acute teeth	Anterior border wide, trun- cated
Xyloryctes ensifer	Narrow; without condyla	Apex rounded, without teeth; molar area small	With 2 acute teeth	Anterior border narrow, rounded

Table 2. Characters in third-stage larvae of six species of Dynastinae (modified from Ritcher 1966; Morón 1976; Morón and Deloya 1991).

SPECIES	Postscissorial tooth (S ₄) of left mandible	Maxillary stridulatory teeth	Shape of holes in respiratory plate	Haptomeral process	Size of abdominal spiracles I-VIII
Cyclocephala imma- absent culata	absent	truncate	oval	notched	VII-VIII large
Ancognatha manca	present	truncate	ameboidal	entire	similar
Coscinocephalus te- pehuanus	absent	rounded	ameboidal	entire	similar
Orizabus brevicollis	absent	sharply pointed	oval	entire	decreasing I-VIII
Ligyrus gibbosus	present	truncate	irregular?	entire	I and VIII small
Xyloryctes thestalus	absent	truncate and sharply	oval, irregular	entire	VIII small
		pointed			



Figs. 1–7. *Coscinocephalus tepehuanus* n.sp. holotype & 1) Right mandible, dorsal view. 2) Labium, ventral view. 3) Labrum, dorsal view. 4) Right maxilla, dorsal view. 5) Parameres, caudal view. 6) Genital capsule, lateral view. Fig. 7) Genital plates (allotype) of *C. tepehuanus*, ventral view. Scale line = 1 mm. Most of mouthpart setae have been removed for clarity.

tose galea fused to small, unarmed lacinia; stipes with groove laterally for reception of retracted maxillary palp; palpus with 4 segments, 1st segment short, 2nd segment about 4 times length of first, 3rd segment 3 times length of first, 4th segment a little shorter than 2nd and 3rd segments combined and with longitudinally depressed sensory area on dorso-lateral surface extending from near base to just past middle of segment (over half length of segment). *Pronotum:* Surface punctate, extremely finely shagreened between punctures; punctures moderate in density and size on posterior half, larger and denser in anterior half and along sides where some become rugopunctate. Sides evenly rounded, widest at middle. Sides and base with marginal bead. Scutellum minutely shagreened, lacking punctures. *Elytra:* Surface with 6 rows of punctate, furrowed striae between suture and humeral umbone and 4 distinct rows

of punctate striae on sides; punctures of striae moderate in size, subequal in size to those in posterior angle of pronotum, weakly ocellate. Intervals weakly convex, minutely shagreened, with irregularly spaced, sparse micropunctures. *Pygidium:* Prepygidium densely punctate. Pygidium regularly convex, surface with sparse, moderately sized punctures on disc, extreme base and angles weakly rugopunctate. *Venter:* Thoracic sternites with moderately dense, long, fulvous setae. Abdominal sternites each with transverse row of setae at about middle. Prosternal peg long with blunt apex covered by long setae. *Legs:* Foretibiae tridentate, teeth subequally spaced. Foreclaws slender, simple. Posterior tibiae with 8 small denticles at apex. All femora with 4 rows of setae (1 dorsal, 1 ventral, 1 on each margin). All tibiae each with 2 rows of setae on dorsal surface. Tarsi subequal in length to respective tibiae. *Parameres* (Figs. 5–6): Slender, symmetrical, with small lateral tooth just past middle of shaft. Venter with long setae in apical half on ventral aspect.

Allotype: Length 24.0 mm from apex of clypeus to apex of elytra; width across humeri 11.3 mm. As holotype except in the following respects: Color dark reddish brown. *Head:* Surface sculpturing a little more coarse. Boss on top of head stronger, a little higher. Apical segment of maxillary palpus with sensory depression less than half length of segment. *Pygidium:* Surface only weakly convex. *Legs:* Tarsi shorter than respective tibiae. *Genital plates* (Fig. 7): Ventral plates rounded, rugopunctate, covered with many long, stout setae.

Variation: Males (2 paratypes) (Fig. 8): Length 22.5–23.0 mm; width across humeri 11.5–12.0 mm. Color varies from light to dark reddish brown. Boss on frons a little stronger in both specimens than in holotype, elytral striae more furrowed. Females (2 paratypes): Length 24.0 mm; width across humeri 12.0 mm in both specimens. Both female paratypes are similar to the allotype.

Remarks: Coscinocephalus tepehuanus is most readily separated from C. cribri-frons by the characters listed in the key. The differences observed between these two species are indicative of recent separation and isolation of one species in the mountains of southeastern Arizona, Sonora, and Chihuahua from the much more southerly species in southeastern Durango. This scenario correlates well with the Pleistocene climatic events that permitted elevational lowering of vegetation. One result of this was that taxa living in the pine/oak associations of the Sierra Madre Occidental in Mexico were able to expand northward to the discontinuous mountains of southern Arizona. Subsequent warming and aridity reestablished the higher elevational gradient supporting pine/oak forests, which effectively created mountain islands harboring, at higher elevations, pine/oak forest (with its associated fauna) in a surrounding sea of lower elevation desert. See Jameson (1990) and Ratcliffe and Deloya (1992) for further information and references on climatic change.

We suggest that the ancestors of both species of *Coscinocephalus* dispersed and subsequently became isolated from one another in this way. Morphological divergence is not yet substantial between the two species due to the relatively recent isolation event. Nevertheless, differences in body structure are already evident, and geographical (hence, reproductive) isolation is now complete.

The limited number of specimens of *Coscinocephalus* collected in Chihuahua and Sonora are conspecific with the Arizona populations even though there is an absence of any mountains high enough to support pine/oak forests between those in southern Arizona and the north end of the Sierra Madre (about 31°N) in Mexico. Deep can-

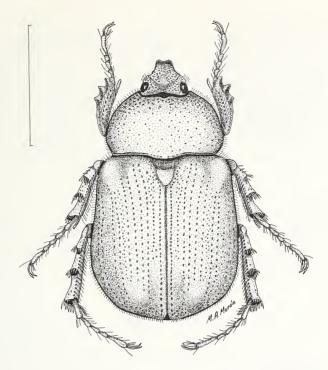
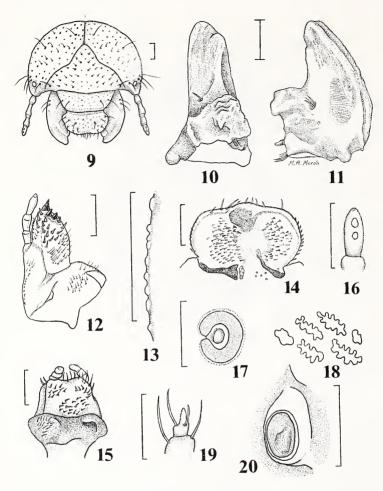


Fig. 8. Habitus of Coscinocephalus tepehuanus n. sp. paratype &. Scale line = 10 mm.

yons formed by the higher tributaries of Rio del Fuerte and Rio Mezquital (22°–27°N) probably restrict the distribution of *C. tepehuanus* to the southern Sierra de Tepehuanes, Sierra de Durango, or only to the Sierra de Michis (Fig. 21). We predict that *C. tepehuanus* should be found in other areas of southern Durango because suitable habitat exists (dry pine/oak forest). A lack of collecting accounts for the absence of additional specimens of this new species.

Etymology: Derived from *tepehuan*, meaning "the owner of the mountains" (Simeón, 1988). Tepehuans are an ancient, native people of the Nahua language group who still live in some parts of the mountains of Durango.

Third-stage larva: Head: Maximum width of head capsule 7 mm. Surface of cranium deeply and sparsely punctate, reddish brown. Frons (Fig. 9) with short, fine, sparse setae; each anterior angle of frons with 1 seta; remaining cranial surface with 1 epicranial seta, 1 dorso-epicranial seta, 1 paraocellar seta and 2 supraocellar setae, and some short, fine, sparse setae on each side. Clypeus with 4 lateral setae. Labrum ovate, slightly asymmetrical, with 2 central setae and 2 lateral setae on each side. Ocelli present, not pigmented. Epipharynx (Fig. 14) with haptomeral process entire, very prominent and sclerotized, without posterior setae; chaetoparia with few sensilla; right chaetoparia with 50–60 spinelike setae; left chaetoparia with 40–45 spinelike setae; right acanthoparia with 6 short, spinelike setae; left gymnoparia with 11 short, curvate setae; right gymnoparia wide, without plegmatia; left gymnoparia



Figs. 9–19. *Coscinocephalus tepehuanus* n.sp. third-stage larva. 9) Frontal view of cranium. 10) Right mandible, mesad view. 11) Left mandible, ventral view. 12) Left maxilla, dorsal view. 13) Stridulatory area of maxilla. 14) Epipharynx. 15) Labium-hypopharynx. 16) Last antennal segment. 17) III left abdominal spiracle. 18) Form of holes in respiratory plate. 19) Claw of left posterior leg. Fig. 20. *C. tepehuanus* pupa, II left abdominal spiracle. Scale lines = 1 mm.

narrowed; acroparia with 4–5 setae; pedium wide; sense cone with 4 sensilla; laeotorma curved toward center of pedium; mesal portion of dexiotormae expanded and fused with the sclerotized plate. Scissorial area of right mandible (Fig. 10) with 2 teeth before scissorial notch and with rounded projection on inner margin; molar area with 3 irregular lobes. Scissorial area of left mandible (Fig. 11) with entire cutting blade before scissorial notch; inner margin with 2 rounded, small projections; molar area with well developed distal lobe (M1); acia acute; brustia well developed; ventral stridulatory area extended, with 35–38 transverse ridges; mesad of stridulatory area is a puncture with 3 stout setae. Galea with well developed, conical, sharply

pointed uncus (Fig. 12); lacinia with 3 terminal unci fused at bases, the inner slightly shorter than others. Maxillary stridulatory area with 8-9 truncate-rounded, small teeth and with a rounded anterior process (Fig. 13). Hypopharyngeal sclerome asymmetrical, strongly produced on right side into rounded process (Fig. 15). Dorsal surface of last antennal segment with 2 oval, small, sensory spots (Fig. 16). Thorax: Thoracic spiracles 0.72 mm long and 0.91 mm wide; respiratory plate reddish brown, shaped as a closed "C"; lobes of respiratory plate nearly approximate; spiracular bulla prominent, rounded. Pronotum with well marked, reddish-orange, irregular formed, lateral scleromes with 2 slender fine setae. Dorsa of meso- and metathorax without setae. All legs with similar tarsal claws, claws pointed, each with 1 internal and 1 external basal setae (Fig. 19). Abdomen: Abdominal spiracles 0.70 mm long and 0.89 mm wide. Respiratory plate reddish brown, regularly shaped as a closed "C"; lobes of respiratory plate closely approximate (Fig. 17), with a maximum of 38-43 irregular shaped, ameboid "holes" along any diameter (Fig. 18); spiracular bulla prominent, rounded. Chaetotaxy on dorsum of each segment as follows: I LS1(4): II LS2(2-10),SS4-5(10-16); III-V LS2-3(2-12),SS4-5(20-24); VI LS1(10),SS4-5(20-24); VII-VIII LS1(2); IX-X LS1(6). Venter of segments I-X each with 4LS. Raster without septula and palidia. Lower anal lip with 70-86 medium sized, spinelike setae. Upper anal lip with 26-40 short, spinelike setae and 10-12 long, slender setae.

Pupa: Body shape elongate, oval, stout, exarate. Color reddish orange. *Head:* Head bent sharply beneath thorax, mouthparts directed ventrally; antennae, mandibles, palpi, and compound eyes recognizable. Anterior border of clypeus slightly tumid. *Thorax:* Pronotum nearly transverse. Pterotecae closely appressed, curved ventrally around body, extending posteriorly between abdominal segments II–III. Protibiae with 3 rounded projections on exterior margin. Tarsomeres delineated. *Abdomen:* 9 visible segments. Spiracles of segment I ovate, slightly prominent, hidden by elytra and by oblique pleural fold; spiracles on segments II–IV ovate, annulate, sclerotized, prominent as rounded tubercles (Fig. 20); spiracles on segments V–VIII occluded, rosetiform, not prominent, sclerotized or pigmented. Tergal area of segments I–VI with 5 pair of deep, moderately sclerotized dioneiform organs (*sensu* Costa *et al.* 1988). Last segment with 2 symmetrical, ventrolateral folds; without urogomphi; last sternite and genital ampulla hidden by folds.

KEY TO THE SPECIES OF COSCINOCEPHALUS (ADULTS)

- 1. Color light to dark reddish brown. Elytral striae on disc with weakly ocellate punctures, punctures subequal in size to those in posterior angle of pronotum. Clypeus with lateral edge sinuate between apex and eye canthus. Southeastern Durango, México

Life history: Coscinocephalus cribrifrons is uncommonly encountered although it may be locally abundant. Part of the reason for its seeming rarity is the fact that adults have a brief period of frenetic activity only at dusk, and they are not strongly attracted to lights. On certain nights after the onset of the late summer rains, males

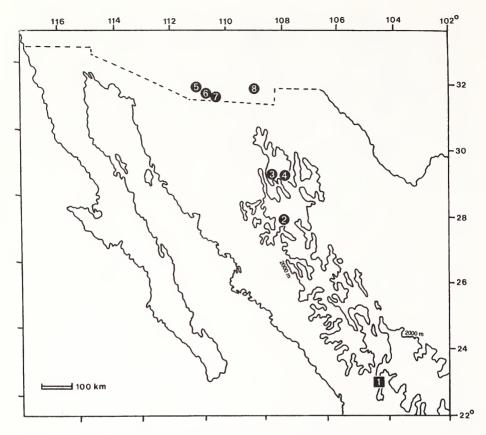


Fig. 21. Known distribution of *Coscinocephalus* species. *C. tepehuanus*: (1) La Michilía, Durango. *C. cribrifrons*: MEXICO: Chihuahua: (2) Creel; (3) Madera; (4) Yepomera; USA: Arizona: (5) Santa Rita mountains; (6) Patagonia mountains; (7) Huachuca mountains; (8) Chiricahua mountains. Base map of northwest Mexico adapted from García & Falcón (1974).

form what are probably mating aggregations. They swarm to a certain tree (Ratcliffe has observed them on pine trees) where they rapidly run up and down the trunk with an audible scritching noise as their tarsi move over the bark. Warner (personal communication to Ratcliffe, November 1994) observed the males gradually ascending to the top of the tree where, presumably, a female or females were releasing pheromones. *Coscinocephalus tepehuanus* probably has similar habits.

We know very little of their life history. The slightly elongated legs seem to us to be an adaptation for their arboreal activities related to mating. We know little of the larvae. Two larvae of *C. tepehuanus* were found in the soil near the roots of a dead oak tree. It is interesting to note that the larvae of *Xyloryctes jamaicensis* (Drury) have been found beneath leaf litter in the soil feeding on roots or microrhizae (Ratcliffe 1991) as have the larvae for *X. thestalus* Bates (Morón 1976). The larvae of *Coscinocephalus* species may be feeding on the roots of live oak trees.

1 Raster with palidia and sentula

The mouthparts of the adults suggest a soft diet such as sap or perhaps pollen. There are no teeth on the mandibles and maxillae for cutting or chewing, and the labrum is reduced. If we eliminate the sap of pines (*Pinus* spp.) as having too many unpalatable secondary compounds, the next most likely sources of food in these habitats are Fagaceae and Erycaceae: oaks (*Quercus* spp.), madrones (*Arbutus* spp.), and "manizallas" (*Arctostaphylos* spp.).

KEY TO THE AMERICAN GENERA OF PENTODONTINI BASED ON KNOWN THIRD-STAGE LARVAE lifted from Pitcher 1966: Morén 1976: Morén & Dalova

(Modified from Ritcher 1966; Morón 1976; Morón & Deloya 1991; Lumaret 1991; Morelli 1992)

1. Raster with palidia and septula
1'. Raster without palidia and septula
2. Palidia monostichous, nearly parallel, each palidium consisting of 7–10 strongly com-
pressed pali whose tips are slightly hooked. Last segment of antenna with 2 dorsal
sensory spots. Ocelli present. Surface of cranium chestnut brown. Maximum width of
head capsule 4.37 mm
2'. Palidia polystichous, each palidium consisting of a patch of 5–7 irregular, longitudinal
rows of sharp, cylindrical, spine-like setae. Palidia and septula extending across lower
anal lip. Last segment of antenna with 2–4 dorsal sensory spots. Ocelli present. Surface
of cranium reddish. Maximum width of head capsule 6.5 mm Ligyrus (Ligyrodes)
3. Inner margin of left mandible (between scissorial and molar areas) with a small tooth
4
3'. Inner margin of left mandible smooth between scissorial and molar areas 8
4. Last antennal segment with 2 dorsal sensory spots
4'. Last antennal segment with 5–8 dorsal sensory spots
5. Spiracles of abdominal segments I–VIII similar in size
5'. Spiracles of abdominal segments I and VIII slightly smaller than those of abdominal
segments II-VII, which are similar in size. Surface of cranium light brown, slightly
roughened, reticulate, without distinctive pits. Maximum width of head capsule 4.8
mm Ligyrus (s.str.)
6. Color of cranium yellowish-brown, surface with numerous small pores. Each side with
1 prominent, exterior frontal seta. Ocelli vague. Maximum width of head capsule 3
mm
6'. Color of cranium reddish brown, surface deeply and sparsely punctate. Each side with-
out exterior frontal setae. Ocelli present, well defined. Maximum width of head capsule
7 mm
7. Epicranium with a transverse, roughened carina extending to supraocellar areas. Last
antennal segment with 5–6 dorsal sensory spots. Ocelli absent. Surface of cranium
dark brown. Maximum width of head capsule 4.7 mm Neoryctes
7'. Epicranium smooth. Last antennal segment with 8 dorsal sensory spots. Ocelli small.
Surface of cranium reddish brown. Maximum width of head capsule 7.2 mm
No. 1 and the state of the stat
8. Last antennal segment with 1–2 dorsal sensory spots. Spiracles of abdominal segments
I-IV similar in size; those of abdominal segments V-VIII progressively smaller pos-
teriorly. Frons with dense covering of setae
8'. Last antennal segment with 4–5 dorsal sensory spots. Spiracles of abdominal segments
I-VIII similar in size. Frons with sparse, short setae only in anterior half. Surface of
cranium chestnut brown. Maximum width of head capsule 6.8 mm Philoscaptus

- 9. Maximum width of head capsule 6-6.5 mm. Distance between lobes of respiratory plate of spiracles much less than dorsoventral diameter of bulla Orizabus
- 9'. Maximum width of head capsule 3.8–5.2 mm. Distance between lobes of respiratory plate of spiracles slightly to much less than dorsoventral diameter of bulla Aphonus

ACKNOWLEDGEMENTS

Roberto Terrón (UAM-Xochimilco, México City) is thanked for collecting and donating the larvae of *C. tepehuanus*. We thank Carl Olson (University of Arizona), Scott McCleve (Douglas, AZ), and William Warner (Chandler, AZ) for locality records, and the assistance of two anonymous reviewers. Partial support of this article is provided by the project "Atlas de Coleoptera Scarabaeoidea de México" (FB067/P134/93 CONABIO-México).

LITERATURE CITED

- Arnett, R. H., Jr. 1968. The Beetles of the United States. American Ent. Inst., Ann Arbor. 1,112 pp.
- Arrow, G. 1937. Coleopterorum Catalogus, vol. 21, pars 156, Scarabaeidae: Dynastinae. W. Junk, Berlin. 124 pp.
- Bates, H. W. 1888. Biologia Centrali-Americana, Insecta, Coleoptera vol. 2, part 2, p. 296–336.
- Blackwelder, R. E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America, pt. 2. Bull. U.S. Natl. Mus. 185:189–341.
- Burmeister, H. 1847. Handbuch der Entomologie, band 5. T.C.F. Enslin, Berlin. 584 pp.
- Casey, T. L. 1915. A review of the American species of Rutelinae, Dynastinae and Cetoniinae. Mem. Coleop. 6:1–394.
- Costa, C., S. A. Vanin, S. A., and Casari-Chen. 1988. Larvas de Coleoptera do Brasil. Mus. Zool. Univ. São Paulo. 282 pp. (165 plates).
- Endrödi, S. 1969. Monographie der Dynastinae. 4. Tribus: Pentodontini. Ent. Abh. Mus. Tierk. 37:1–145.
- Endrödi, S. 1985. The Dynastinae of the World. Dr. W. Junk, Dordrecht. 800 pp.
- García, E. and Z. Falcón. 1974. Nuevo Atlas Porrúa de la República Mexicana. Ed. Porrúa, México. 197 pp.
- Jameson, M. L. 1990. Revision, phylogeny and biogeography of the genera *Parabyrsopolis* Ohaus and *Viridimicus*, new genus (Coleoptera: Scarabaeidae: Rutelinae). Coleop. Bull. 44:377–422.
- Leng, C. W. 1920. Catalogue of the Coleoptera of America, North of Mexico. John D. Sherman, Mount Vernon, NY. 470 pp.
- Lumaret, J. P. 1991. Le genre Neoryctes Arrow, 1808: description de la larve et position taxonomique du genre (Coleoptera: Scarabaeoidea: Dynastidae: Pentodontini). Elytron 5:337–341.
- Morelli, E. 1992. Taxonomía de los estados immaduros edafícolas de coleópteros dinástidos (Tribus: Cyclocephalini, Oryctini y Phileurini) del Uruguay. Tesis de Maestría en Biología, Zoología. Universidad de la República, Montevideo, Uruguay. 123 pp.
- Morón, M. A. 1976. Descripción de las larvas de tres especies mexicanas de melolontinos (Coleoptera, Melolonthidae: Dynastinae y Rutelinae). An. Inst. Biol. Univ. Nac. Autón. México (ser. Zool.) 47(2):119–134.
- Morón, M. A. 1987. Los estados immaduros de *Dynastes hyllus* Chevrolat (Coleoptera: Melolonthidae, Dynastinae); con observaciones sobre su biología y el crecimiento alométrico del imago. Folia Entomol. Mex. 72:33–74.
- Morón, M. A. and C. Deloya. 1991. Los coleópteros lamelicornios de la Reserva de la Biosfera "La Michilía," Durango, México. Folia Entomol. Mex. 81:209–283.

- Prell, H. 1936. Beiträge zur Kenntnis der Dynastinae. Über Homonymierverhältnisse der Namen der Gattungun und Untergattungun. Entomol. Blätt 32:145–152.
- Ratcliffe, B. C. 1991. The scarab beetles of Nebraska. Bull. Univ. Nebraska St. Mus. 12:1–333.
- Ratcliffe, B. C. and A. C. Deloya. 1992. The biogeography and phylogeny of *Hologymnetis* (Coleoptera: Scarabaeidae: Cetoniinae) with a revision of the genus. Coleop. Bull. 46: 161–202.
- Ritcher, P. O. 1966. White Grubs and their Allies. Oregon St. Univ. Press, Corvallis. 219 pp. Schaeffer, C. 1906. On *Bradycinetus* and *Bolboceras* of North America, with notes on other Scarabaeidae. Trans. Am. Entomol. Soc. 32:249–260.
- Simeón, R. 1988. Diccionario de la Lengua Náhuatl o Mexicana. Siglo Veintiuno, México, D.F. 783 pp.

Received 15 April 1995; accepted 16 October 1996.